SOME ADAPTIVE RESPONSES OF TAXONOMY TO A CHANGING ENVIRONMENT

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Although taxonomy in a very primitive sense long antedates the Linnæan system of binomial nomenclature, its present phase of development is inseparable from this system. Indeed, we may ask whether any other method could have been extended to meet so well the present needs of biological classification. Certainly no acceptable substitute has been proposed through the course of nearly two centuries during which innumerable taxonomists have described and classified, to the best of their ability, more than a million species of animals and plants.

The human race first learned to exploit the bounties of nature by a crude, though astute, knowledge of edible plants and food This demanded an accurate discrimination of the charanimals. acters of many species of plants and to a lesser extent of animals, and served incidentally to create the vague beginnings of pharmacology. The beginnings of taxonomy smouldered for centuries however, even after written language had become an established vehicle for recording complex ideas. It made little progress, in spite of a few sporadic attempts to classify, or at least to describe and place in an orderly arrangement a few of the more conspicuous living organisms.¹ Sometime before the appearance of the Linnæn "Systema Naturæ" the microscope had come into quite general use and the time was ripe for biologists to examine with considerable exactitude the structure of small animals like insects as well as the more minute anatomical details of many living things that had hitherto eluded observation by the naked eye.

If, as seems reasonable, we consider the birth of modern taxonomy as coincident with the publication of the "Systema Naturæ," we find a healthy new branch of science suddenly born after prolonged gestation. Like a newborn organism, its first

¹ These really include only the works of Aristotle, Pliny, Gesner, Aldrovandri, Ray and several botanists who shortly preceded Linnæus.

concern was growth. This involved development, differentiation, adaptation and a number of other phenomena always associated with growth which are familiar to all biologists.

Growth in individual organisms, and in populations, always follows a quite definite and prescribed course. Moreover, this is frequently true of many other types of utterly unrelated events such as the frequency of fundamentally new inventions and the popularity of certain social ideals, of dogmatic beliefs or even of rag-time music or jazz. As this phenomenon of growth is such a universal one, I have attempted to examine the progress of insect taxonomy on a similar basis. We may measure this by an examination of the productions of taxonomists over a period of time.

Since the field is a vast one a high degree of accuracy is impossible, but I have been able to collate with the aid of the "Zoological Record'' a summary of the new names proposed annually by zoologists² over a period of somewhat more than half a century. This is represented in Figure 1 as a curve, the points on the curve being determined arithmetically by the addition of each annual incre-This curve has been smoothed on a three-year basis to ment. reduce the irregularities introduced by the occasional appearance of some magnum opus or even the coincident publication of several such tomes during a single year. The similarity of this graph to a portion of the sigmoid growth curve of an individual animal is very striking. We should, of course, properly tabulate our material for the earlier periods also, but for practical reasons this has been impossible as there are no reliable sources for the necessary data. It would appear that the period we have selected includes the age at which the growth rate is undergoing acceleration, especially when we note the lag from 1914 to about 1920 which is undoubtedly due to the world war, and the rapid, overcompensated recovery after this time. Altogether during the period of sixtyfive years from 1870 to 1934, 103,752 new names were proposed, equivalent to a mean annual increment of almost exactly 1600. The change in rate over the whole period is consistent, but not

² These names include, of course, new names proposed for others which have been invalidated as homonyms, but the number of these is small, and is distributed quite evenly from year to year. The annual totals also include the names later invalidated both as synonyms and homonyms, but this error is inevitable and would appear also to be of no great magnitude. JUNE, 1939]

great and does not bear out the opinion that is frequently voiced by many zoologists that systematics has gone wild with the needless multiplication of generic names. Actually the number of new names proposed annually has approximately doubled after sixtyfive years. This is certainly not out of proportion to the greatly increased number of workers, more abundant materials available and enhanced opportunities for study and publication. Moreover,



FIG. 1. Growth of generic and subgeneric names in use by taxonomists in the entire field of zoology, 1870–1934.

we have good reason to predict that taxonomy may still expect a long and productive life insofar as the recognition of new genera is concerned, and that the maximum growth rate has not yet been reached.

Since insects form the major part of living organisms, that have come under the taxonomist's eye, they should serve as a reasonable guage of systematic biology as a whole. If we now turn to Entomology in particular and construct a similar graph based on the new names proposed for insects over a similar period we see a curve (Figure 2) which is more or less like the preceding one. It differs markedly, however in showing less clearly the sigmoid form,





FIG. 2. Growth of generic and subgeneric names in use by taxonomists in the field of entomology, 1870–1934.

although this is slightly evident, and approaches more closely to a straight line, with a less noticeable disturbance at the time of the war (1914–1920). The reason for this difference from the whole zoological curve may indicate a later stage of growth, although it may be due to some other unsuspected factor, and were it not for the rather characteristic form of the first curve this one might not appear significant. If we turn to several orders of insects and consider these individually over a fifteen year period (Figure 3) we can see nothing but a generally consistent and uneven growth. Here undoubtedly the number of workers is so small that their variable output tends to produce considerable irregularities, and there is no indication that a longer and much more tedious compilation would be worth while. The several orders have not by any means attracted an equal number of workers, nor have they received approximately equal attention, nor is our knowledge of them equally complete, yet none of these variables are sufficiently correlated over a period of years to give any indication of changing or differential growth rates. The only consistent change is a

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FIG. 3. Growth of generic and subgeneric names in use by taxonomists for several orders of insects (Coleoptera, Lepidoptera, Diptera and Hymenoptera), 1920-1934.

gradual, irregular increase in growth rate which holds true for each of the four orders.

As an indication of what might be expected of entomology in the future, I have compared the number of new names proposed



FIG. 4. Growth of generic and subgeneric names for birds and mammals, 1891–1934.

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for birds and mammals over the period of 1921–1934. Since the discovery of new species in these groups is now very greatly reduced over former years we should expect to find an entirely different condition with reference to new generic and subgeneric names. In Figure 4 is plotted the additions for birds and mammals, resulting in a practically straight although wavering line, with no indication that taxonomic complexity depends for its growth on the continued discovery of hitherto unknown forms or organisms! The growth rate is apparently just about holding its own, with no significant increase or decrease. From this we may predict, with a considerable margin of safety, that after all the species of insects are known we shall continue, at least for a time and at a reduced rate, to reclassify, redistribute and redivide them into new genera and subgenera.

I have compiled one other series of data relating to a single restricted group of insects (Figure 5). For this purpose the



FIG. 5. Growth in number of described species of the family Cerambycidæ (sens. lat.).

longicorn beetles (family Cerambycidæ sens. lat.) were selected as these are attractive, usually large beetles that have been very extensively collected and should be much more completely known than most other families of insects. The curve in this case shows the numerical growth of known species as described from year to year from 1870 to the present time. As might be expected this curve is very irregular, due to great annual fluctuations resulting from the comparatively small number of papers that contain descriptions of new species. The growth rate wavers nervously about a nearly straight line, indicating a practically constant rate of increase in the number of known species. Actually the mean annual increment is 168 species, or 10,915 in 65 years.

This great growth of taxonomy, both in the number of its adherents and also in the rapidly increasing size of the complexes with which it deals, has had the inevitable result that follows the extension of any field of knowledge. There has come a gradual and consistent specialization. The entomologists of the earlier period became the coleopterists, hymenopterists, dipterists and orthopterists of the late nineteenth century. These are now gradually giving place to the myrmecologists, coccidologists, cynipidologists, empididologists and tachinidologists, alias larvævoridologists. This has meant a steady narrowing of the field for the individual systematic worker, coincident with the opportunity for a more complete knowledge of his own special field. We are now in this transition period and these changes appear to have been very generally a great gain for taxonomy. We must not forget however that our greatly specialized taxonomists of to-day had a much broader background than we may hope to find in later generations if the young entomologists of the future settle into isolated and comfortable niches before they acquire any first hand knowledge of the matters which engross the attention of their neighbors. We are, of course, referring here only to taxonomy and not to the other phases of biology, but it is a striking fact that among entomologists who are not primarily taxonomists, nearly all find occasion to devote some time to the classification of some group, large or small.

We cannot foresee the future growth of taxonomy as measured by the increasing number of genera and species that may be made known, more than to predict on the basis of the past 75 years that there is no indication that a maximum growth rate has yet been reached, nor that after that time a decline may be promptly expected to follow. Great familiarity with a restricted group of insects or other organisms leads primarily to a better understanding of their similarities and the characters which distinguish them one from another. As they are more critically examined, these contrasting characteristics lead to a clearer recognition of generic grouping and specific segregation, and the natural result is the multiplication of genera and species. This follows consistently among practically all systematists and I do not believe that the designation of "splitters" and "lumpers" is really a valid distinction for the near future. At any rate the gap between proponents of these two types of procedure is now notably lessened, if we discard as non-taxonomic the classification of aberrations and the like among butterflies.

The early taxonomists did their work without any knowledge of organic evolution or of racial descent and consequently without any thought of the possible genetic relationships of living animals to one another and to their many long extinct ancestors. It might be argued that a vague idea of evolution may have influenced Aristotle in his classification of animals wherein he included altogether about 525 species, some of which were imaginary creatures existent only in the minds of their describers. However, any such notions were completely lost to all the later predarwinian taxonomists. Nevertheless taxonomic methods suffered comparatively slight changes following the general acceptance of evolution as a biological principle. This appears at first blush an almost unbelievable situation particularly as it was mainly the work of the taxonomists that gave the original theory its strongest sup-The whole science of biology was rocked to its foundations port. at this period, yet the insect taxonomists went serenely on classifying animals in the same old way with only scant and parenthetical disquisitions on phylogeny and on the newly clarified aspects of relationships. To the minds of non-systematic zoologists this has been a cardinal sin and has led them to regard taxonomy as a pastime closely related to that of the stamp collector. As a matter of fact the phylogenetic approach to relationship was confined to a consideration of the larger categories of animals, and naturally enough also to those groups of much lesser extent than the insects or to those whose classification was not sufficiently advanced to introduce the innumerable difficulties that beset the entomological taxonomist. Herein lies, undoubtedly, the reason for the apparent lack of appreciation on the part of entomologists of the bearing of evolution on the more detailed parts of their schemes of classification. More recently this condition has changed and is in general proceeding from a consideration of the higher categories and gradually ramifying into the smaller ones (families, tribes, genera, etc.). The influence of paleontology on the taxonomy of living animals was first felt after the doctrine of organic evolution had been advanced and has rapidly become highly important, for example, in the classification of reptiles and mammals. In like manner the recent extensive growth of insect paleontology has greatly furthered our knowledge of the relationships of many types of living insects.

The more recent entry of genetics into biology has again greatly changed the environment of taxonomy. Here likewise this new outlook has so far exercised a very slight, almost negligible influence on taxonomic procedure. In a few isolated instances genetical experimentation has served to elucidate the relationship of color varieties and polymorphic forms within species, but it has been thus far so very imperfectly correlated with the more general problems of evolution and speciation that it cannot be applied directly to taxonomic work. It is hardly open to question that genetics will in the future bring its understanding of the gene and the unit character to a stage that will allow of their application to taxonomy. Unforunately, so far genic differences and mutations observed in the experimental sphere are concerned almost entirely with those types of structural peculiarities and deficiencies which cannot be correlated with the specific associations of both constant and variable characters which must form. after all is said and done, the workings basis of taxonomy. We may of course qualify this statement as has often been done by insisting that species are artificial concepts, non-existent in nature, and further that there is no essential agreement among taxonomists as to the limits of particular species. There is good basis for such qualifications in some instances, but it has been greatly overemphasized, and the question has frequently been clouded by a confusion of species, subspecies, geographic races, varietal forms, etc. The latter categories were of little concern to the earlier taxonomists who made use of them in rather loose fashion. However, the recording of more extensive and exact data on the geographical distribution of species and the consequent recognition of the fact that variations may be associated with distributional range over contiguous areas has led taxonomists to enquire more closely into the status of subspecies and races. Thus through cooperation with zoögeography, taxonomy has secondarily entered the field of phylogenetics by a direct path and has become actively interested in the origin of species and higher categories, rather than their mere existence. This appears thus to be a long delayed response of taxonomy to evolution. Long delayed, in that the taxonomists have now begun to accumulate data with this end in view, rather than to furnish material for interpretation by others.

As the oldest branch of biology, taxonomy appears to be the most set in its ways, but even the foregoing brief citation of some of its responses to changes in biological thought demonstrate that it has by no means reached a stagnant condition. It is nevertheless far less labile than most other branches of biology. This is to be expected considering the vast entourage of genera and species with which it is encumbered on its onward march, not to mention the ghosts of their ancestors clamoring for a place in the parade as they are resurrected from the dead by inquisitive paleontologists.